

Fertile-sterile Leaf Dimorphism in Ferns

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In addition to his many other contributions, Dr. R. E. Holttum has been unquestionably one of the world's leading authorities on the taxonomy of ferns with fertile-sterile leaf dimorphism, especially the lomariopsid group. Inspired in part by reading his papers, we became interested several years ago in the over-all subject of fertile-sterile dimorphism and began the study to be reported here. As will be seen, there are numerous disagreements in the interpretations of dimorphism, and this represents an effort to review these as well as other aspects of the general phenomenon.

Dimorphism of fertile and sterile fronds is widespread and bears upon both the systematics and ecology of ferns. It is an expression of a trend found throughout vascular plants, a trend which achieves its ultimate in seed plants. Recognizing that the term "dimorphism" may sometimes apply to other than fertile-sterile (i.e., various types of heterophylly of vegetative leaves in ferns), for convenience the term here will be confined to differentiation into sporophylls (spore-producing fronds, *fertile Blätter*) and trophophylls (purely photosynthetic fronds, *Laubblätter*). Profound alterations may appear in the evolutionary transition from primitive monomorphism, including transformations in morphology, anatomy, physiology, and ecology. These changes are thought to possess adaptive value. However, this idea is not universally accepted, and there is little or no experimental evidence to support it. At present, in fact, most of our conclusions are intuitive and hypothetical, and we strongly need rigorous tests. We hope that the ideas we present here will help to stimulate such experimentation.

As many as one in five of all fern species possess what may be called fertile-sterile dimorphism, but this figure has to be arbitrary because of so many transitions that occur between monomorphism and dimorphism. Where the dimorphic condition is strongly expressed, taxonomists have traditionally utilized it as a useful character in species discrimination. In some instances, taxonomic separations have been created even at the generic level on the basis of sporophyll-trophophyll dimorphism.

The analysis of foliar dimorphism invokes a multitude of biological questions such as what parts undergo changes, what are the effects on sporangial arrangement, what developmental processes underlie formation and timing of fertile expressions, what — if any — ecological advantages are conferred, and to what extent dimorphism is valid as a systematic character. The following report is an outcome of our observations in the field, laboratory, and herbarium, together with a survey of the literature. The most thorough and most recent survey seems to be that of F. G. Dickason in 1946. Because of the widely scattered nature of references to this subject, we fully expect that some important items have been overlooked. We also anticipate that various ideas expressed here will be subjected to future

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reappraisal. If, however, this article serves to stimulate critical research, its purpose would be fulfilled.

All degrees of morphological and anatomical divergence exist between fertile and sterile fronds. In fact, one of the reasons the term "monomorphic" is rarely used may be that practically all ferns are strictly speaking at least slightly dimorphic. Steps in dimorphic divergence are well exemplified in numerous genera. In eastern North America, for example, we encounter a good illustration in the woodfern genus, *Dryopteris*. *D. goldiana* (Hook.) Gray has hardly any detectable difference between soriferous and non-soriferous mature fronds. *D. cristata* (L.) Gray, with erect, tall fertile fronds, and spreading, short sterile fronds, shows strong differentiation. *D. spinulosa* (O. F. Muell.) Watt is intermediate. Other good examples of such sequences are met with over a broad taxonomic spectrum, such as, in Polypodioideae, *Loxogramme*, *Microgramma*, and *Pyrrosia*; in Blechnoideae, *Blechnum*; and in Dryopteridoideae, *Davallia*, *Humata*, *Nephrolepis*, *Oleandra*, and *Polystichum*².

It should be understood that the term "dimorphism" does not necessarily imply a precise morphological parallelism. The changes involved are probably often the result of analogous, rather than homologous, transformations, and different examples show different degrees of involvement of petioles, blades, pinnae, sporangial arrangements, histology, and physiological reactions.

The sporophyll-trophophyll differentiation may embrace whole fronds or only parts of fronds, and in the latter, it may be the tip that is fertile, the middle of the frond, or the base. These modifications are diagrammed in Figure 1. Interfoliar dimorphy, constituting complete differentiation of whole fronds is the most common type. However, because of the commonly transitional nature of the manifestations, many fertile fronds are merely "subdimorphic" (term as used by Dickason, 1946) in the sense that the changes displayed are incomplete in kinds and amounts. A "holodimorphic" situation includes total loss of vegetative function in the sporophyll. However, the latter is hard to achieve because during the early stages of maturation the rachises and costae of all fertile fronds (at least those known to us) are to some extent green and photosynthetic. Whole-frond differentiation into sporophylls may follow two routes. It may be the culmination of an evolutionary trend in which at first only the frond tip is fertile. Dickason (1946) suggests that there is a progressively earlier shift from the vegetative to the reproduction condition of the leaf starting at the apex (i.e., Fig. 1, B to D) mediated by an hypothetical "sporogen" growth substance. On the contrary, one can just as well imagine modification of the whole leaf progressing from the inception of the leaf, bottom to top.

Where fertile-sterile differentiation appears in separate parts of the same leaf, "the term *hemidimorphism* is used instead of *dimorphism*" (Dickason, 1946). The hemidimorphic leaves with terminal fertile pinnae are the most widespread. In Osmundaceae, this condition is illustrated by the familiar *O. regalis* L.; in Polypodioideae, by the genera *Paltonium* and especially *Belvisia*; in Grammitidoideae, by *Grammitis* Sect. *Xiphopteris*; and in Adiantoidae, by *Llavea*. Two extremes in the Dryopteridoideae are observed in the eastern North American *Polystichum acrostichoides* (Michx.) Schott and *Dryopteris ludoviciana* (Kze.) Small. As in other forms of hemidimorphism, the fertile pinnae — even when they are photosynthetic at the time of spore production as they are in *D. ludoviciana* — are shorter-lived than the sterile, and turn brown and die well before the sterile pinnae.

Examples of hemidimorphism in which only the medial pinnae are the fertile ones are known best in *Osmunda*, and most familiarly in *O. claytoniana* L., which is designated in North America by the colloquial name of "interrupted fern"

² The family-subfamily classification used in this paper is that of W. Wagner (1973).

because its fertile pinnae discharge their spores and fall off early in the season (usually by early or middle July), leaving fronds in which the lower and upper regions of photosynthetic pinnae are set apart by a length of naked rachis.

Ferns with the hemidimorphic condition effecting only basal pinnae are taxonomically a motley lot. In the striking cyatheoid genus *Thyrsopteris*, known in the living flora only from Juan Fernandez Islands, several pairs of lower pinnae are fertile, these extremely skeletonized (i.e., lacking lamina) but bearing sori with conspicuous cup-like indusia. More abundant ferns with modified basal pinnae occur in Ophioglossaceae and Schizaeaceae subg. Anemioideae. In the genus *Anemia* we find a spectrum running from only subtly subdimorphic basal pinnae all the way to fully differentiated basal pinnae. Accompanying this progressive laminar reduction and skeletonization of the basal pinnae pair, there is increased tendency for them to become erect and tower above the spreading sterile pinnae. In the most evolved forms in *Anemia*, the sporangial masses are held well above the photosynthetic portions of the leaves, and effectively the same result is achieved as in those dimorphic leaves in which the sterile fronds are flat and form rosettes (cf. Fig. 1, C, hemidimorphic, with Fig. 2, D, holodimorphic). The alterations in *Anemia* have been described in some detail by Mickel (1962, 1967). One of the interesting features in specialized members of this genus is the close association of the fertile basal pinnae in point of apparent origin with the second pair of pinnae, i.e., the lowest of the sterile pinnae, a condition to which Mickel refers as "fertile pinnae approximate to sterile." On the basis of comparative morphology, we can conclude that the fertile petiolule bases have fused with the main petiole up to the first sterile petiolules. A parallel condition is seen in the single fertile spike of certain Ophioglossaceae, e.g. *Botrychium virginianum* (L.) Sw.

Mickel (1967) describes the probable evolution of the fully fertile fronds of certain species of *Anemia* as following a pathway opposite that suggested by Dickason (see above) for other holodimorphic ferns. Most *Anemia* taxa produce a single pair of fertile basal pinnae, but in *A. rutifolia* Mart. there is more than one pair of basal fertile pinnae, and in *A. millefolia* Gardn. all of the pinnae are fertile. We do not believe that the two models are necessarily in conflict, nor the idea, suggested earlier, that in some cases the sporophyll may have been holodimorphic from the beginning. There are thus three different possible routes: (a) change directly from monomorphic leaves to holodimorphic (Fig. 1, A-D); (b) change from monomorphic to hemidimorphic, with the fertile pinnae apical, to holodimorphic (Fig. 1, A-B-D); and (c) from monomorphic to hemidimorphic with the fertile pinnae basal to holodimorphic (Fig. 1, A-C-D). Monographers should be prepared to encounter any one of these routes in a given evolutionary line.

Morphologically the single fertile spike of Ophioglossaceae (*Botrychium*, *Helminthostachys*, *Ophioglossum*) resembles the fertile basal pinna condition in *Anemia*, differing from it in the apparent fusion to form a single primordium and mature structure. This interpretation — the "Fusion Theory" or "Peltation Theory" — to explain the fertile spike, is the most parsimonious and requires the least number of assumptions³. Unfortunately, the morphological intermediates that would directly confirm the phylogeny of the fertile spike have been lost from the fossil record. All we have are data from living forms to support this interpretation — the pattern and origin of vascular strands, and the occasional grapefern specimens (especially in *Botrychium* subg. *Sceptridium*, considered primitive on other grounds) of the *Anemia* condition with separate fertile basal pinna pairs, as

³ In the welter of interpretations to which the fertile segment of Ophioglossaceae has been subjected, one of the most unusual is that of Wieffering (1964), who, regarding *Ophioglossum*, treats the sterile segment of the frond as a "trophophyll" and the fertile spike as comprising a "fertile stalk" terminated by a "strobilus"!

well as intermediates. There are a few examples of adder's-tongue ferns, *Ophoglossum*, with the sterile blade reduced or suppressed entirely. However, the belief that the rare South African species, *O. bergianum* Schlecht. has complete sporophyll-trophophyll separation (as believed, for example, by Copeland, who keyed it out on this basis in 1947) has proved to be erroneous. In our own observations of this curious plant we find an illusion of two separate fronds that is created by a very low attachment of the fertile spike to the sterile segment.

Although the details are not agreed upon, the consensus seems to be that the sporocarps of the Marsileaceae are modified basal pinnae in which the sporangia are encapsulated. Unless it can be established that the sporocarps are *de novo* in origin, comparative morphology dictates that the homology to basal pinnae is the most likely explanation of these very distinctive structures, especially if it is agreed that Marsileaceae are specialized leptosporangiate ferns. Gupta (1956, 1962) has brought together much of the information bearing upon the nature of the sporocarp. Also, he has found (pers. comm.) very interesting forms of *Marsilea minuta* L. which have numerous sterile pinnae borne along the leaf axis, suggesting a reversal to a more primitive condition. It is easy to speculate that the hemidimorphic condition of Marsileaceae may have more than a coincidental resemblance to that of the Anemioideae.

Attention should be called to the less spectacular but substantial changes that often occur in the specialization of distinct trophophylls. The obviously striking aspect of many sporophylls quickly attracts attention from morphologists and taxonomists, but often the trophophylls themselves do not remain merely as sterile remnants but little changed from the original double-duty leaves of the monomorphic ancestors. The uncommon curly-grass fern, *Schizaea pusilla* Pursh, of northeastern North America has trophophylls which are wiry, twisted organs concentrated at the base of the plant. In various polypodioid genera, such as *Microgramma* in the New World and *Pyrrosia* in the Old, there seems to be an inverse correlation between changes in the sporophyll and those in the trophophyll: As the sporophyll becomes longer and narrower, the trophophyll becomes shorter and wider. Holttum (1954) illustrates *Pyrrosia nummularifolia* (Sw.) Ching, an extreme example in its genus with the sterile fronds "very shortly stalked, almost circular to broadly ovate." In this example, the fertile fronds are more similar to the norm of the non-dimorphic or subdimorphic fronds of the genus than are the sterile. Figure 2, D, illustrates this type of change in trophophylls.

In a few of the paddle-ferns, *Elaphoglossum*, the trend described above is reversed: The trophophylls become linear, extremely long and narrow, and pendent, while the sporophylls retain their lanceolate outlines. Splendid illustrations of such specialized hanging trophophylls are the New World tropical *Elaphoglossum siliquoides* (Jenm.) C. Chr. and especially *E. herminieri* Bory ex Fée.

In teleological terms, the "need" for certain leaf shapes required by carrying out both duties of photosynthesis and sporulation seems to be eliminated if sporophylls evolve, permitting the trophophyll to become more adapted to its role. In *Dryopteris cristata*, the sterile leaves are smaller and more spreading, so that they form a "light-catching" rosette at the base of the plant in contrast to the bulk of the species of *Dryopteris* in which the sterile fronds are less differentiated from the soriferous fronds. In general, in terrestrial forms, the flatter and rounder the trophophyll, the more efficient it will be photosynthetically. This seems to be true also in those epiphytic ferns, such as the creeping polypodioids, in which the trophophylls "hug" the branches and twigs of the host trees and shrubs.

A somewhat neglected component of comparative morphology of the sporophyll is the modification of sporangial distribution. The over-all trend is toward the concentration of sporangia, but this concentration is achieved in a variety of ways. The sori may keep their organization and simply become more tightly grouped.

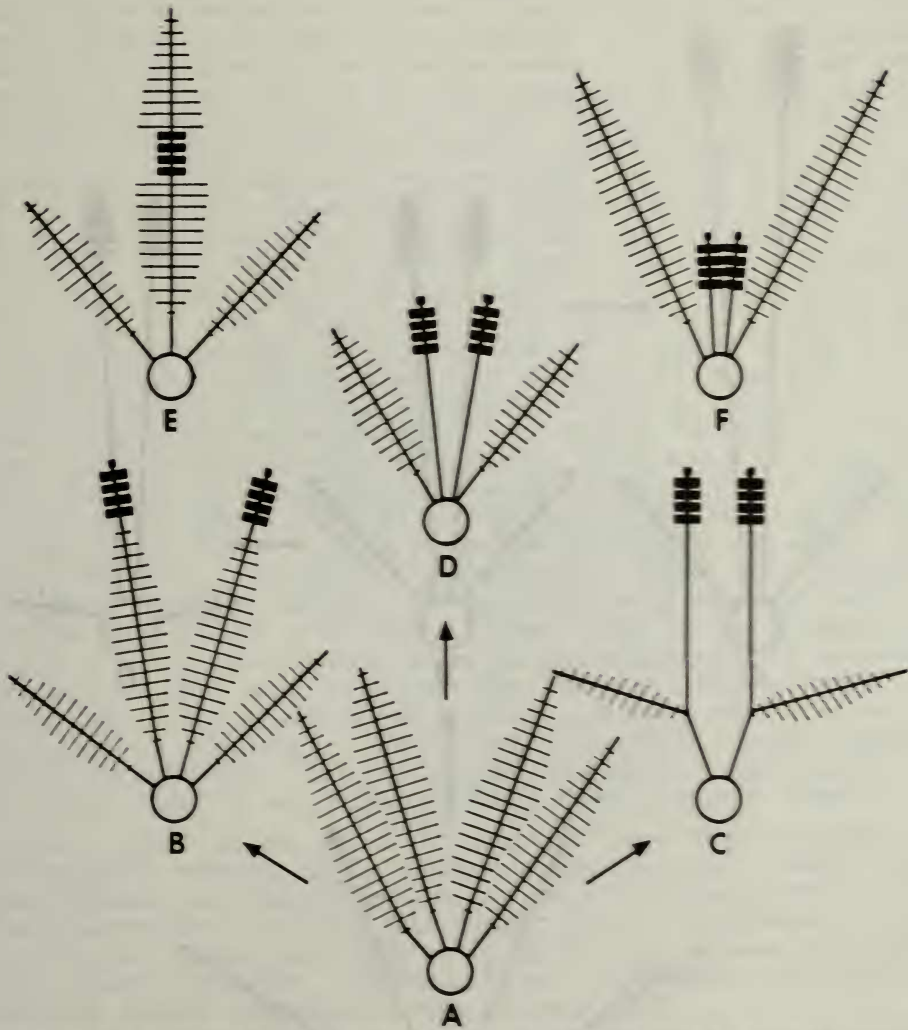


Figure 1. Diagrammatic representation of fertile-sterile dimorphism. *A*. Primitive condition: monomorphic. *D*, *F*. Complete dimorphism of sporophyll and trochophyll, showing different relative sizes of sporophylls. *B*, *C*, *E*. Hemidimorphic conditions: *B*. Fertile parts terminal. *E*. Fertile parts medial. *C*. Fertile parts basal.

They may, on the other hand, lose their soral organization and fuse into a continuous "sheet" of sporangia spread over the sporophyll lamina, or the entire sporangial area may become skeletonized, losing laminar webbing completely and producing clusters of single-veined axes. The sporangia may be exposed, even in the youngest stages of development (as in certain acrostichoid ferns), or they may be protected by indusia, paraphyses, or by inrolling of laminar tissue to form more or less persistent sheltering capsules. Also, these various modifications may be combined in different ways.

Compacted but still discrete sori are observed in diverse taxonomic groups. The exposed epidermal areas between the sori are reduced so that finally no bare epidermis can be seen and the sori are in contact on all sides. For polypodioid sori this is well illustrated in the genus *Pyrrosia*. While it is true that after spore discharge members of this genus may appear to have truly acrostichoid soriation,

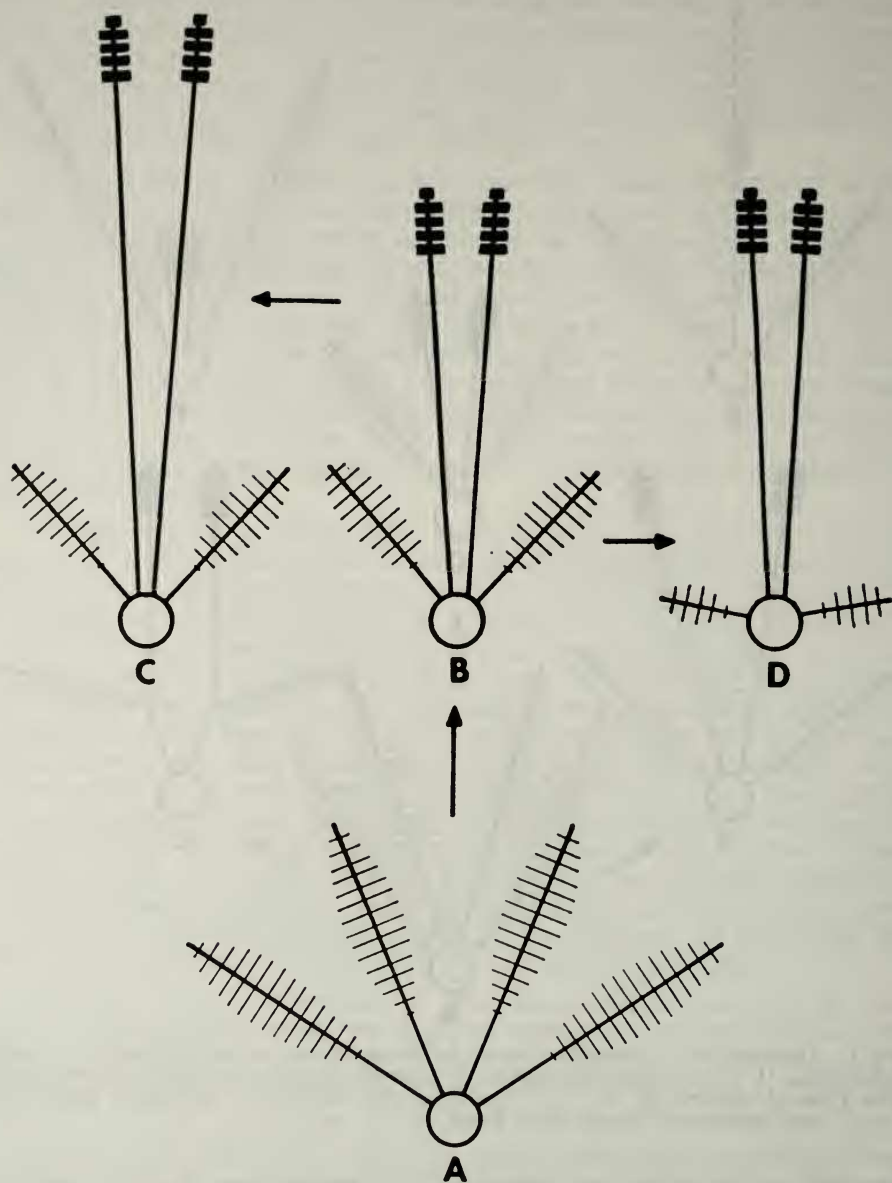


Figure 2. Diagrammatic representation of relative differentiation of sporophylls and trophophylls. *A*. Primitive condition: monomorphic. *B, C, D*. Dimorphic. *C*. Extreme change in sporophyll, the characters (height, orientation, exaggerated). *D*. Extreme change in trophophyll, specializations of size, shape, and orientation strong.

this is actually an illusion. Sori of the ancestors of *Pyrrosia* were probably of the type seen today in *Pleopeltis* — well separated, exindusiate, and round. An outstanding example of nearly confluent indusiate sori is present in the eastern North American *Polystichum acrostichoides* (L.) Schott. Here the situation resembles that in *Pyrrosia* in that after spore discharge the fertile pinnae become falsely acrostichoid. Prior to spore discharge, however, not only are the discrete sori recognizable, but each is provided with a conspicuous peltate indusium.

Truly acrostichoid soriation results from the origin of sporangia upon a continuous placental surface which extends across the abaxial surface of the blade or pinna. Even in young stages it is not possible to make out individual sori. Although there are some disagreements over details of interpretation and terminology (cf. W. Wagner, 1965, pp. 299, 300), recognition of this type of soriation is generally accepted as a valuable tool in generic taxonomy. Ferns with acrostichoid soriation may or may not have laminar contraction associated with it. In *Elaphoglossum* (Aspleniaceae subg. Dryopteridoideae) and *Acrostichum* (Adiantaceae), the fertile blades or pinnae may be only slightly contracted or not contracted at all. However, they tend to be more ephemeral than the sterile blades or pinnae, becoming curled and dry before the sterile segments. Acrostichoid soriation in unrelated taxa probably has had different modes of origin. In *Acrostichum* the ancestors were very likely gymnogrameoid ferns lacking indusia. The sori were linear and followed the veins, and they were separated by exposed laminar surface. By extension of the sori into the naked areas and finally becoming confluent, the acrostichoid condition came about, the sporangia making up a continuous sheet, clothing the entire laminar undersurface. On the contrary, the history of *Elaphoglossum* may have followed a very different route. If we accept the comparative evidence from many characters, *Elaphoglossum* is a derivative of ferns with round, indusiate sori (like those of *Dryopteris* and *Polystichum*). The steps in the evolution of *Elaphoglossum* from its probable progenitors may then be suggested to have followed this route: (1) assumption of the epiphytic habitat, (2) simplification of the frond, divided to undivided, (3) approximation of sori, from remote to continuous (as seen today in *Polystichum acrostichoides*), (4) loss of indusia, and (5) unification of placental tissue all across the laminar surface to become acrostichoid. Some of these steps may have taken place in a different order. The important point is that the acrostichoid condition may be the result of convergent evolution and not necessarily be a signal of systematic affinity. Surely the examples known in the polypodioid ferns (e.g., *Belvisia*, *Christiopteris*, *Dendroglossa*, and *Platyserium*) arose from very different ancestors from those given above.

Bower pointed out long ago (1923) that some acrostichoid ferns have "no special vascular provision for the nutrition of the sporangia", whereas others develop elaborate modifications involving two parallel vascular systems — the normal venation plus a specialized receptacular venation on the abaxial side. The two are in connection with each other, of course. The state of having two parallel vascular systems is termed "diplodesmic", and is especially well shown by acrostichoid examples in the Polypodioideae (Bower, 1928).

What we here call the *botryoidal condition*, in which the sporangia form clusters upon more or less naked and branched axes, is best shown in three groups — Ophioglossaceae, Schizaeaceae subg. Anemioideae, and Osmundaceae. Here the flat laminar condition is partially or entirely lost, and the sporangial masses become three-dimensional and glomerulate. Assuming that lamina-borne sporangia are ancestral (see discussion below) we may conclude that the primitive condition in Osmundaceae is that displayed by *Todea* and in Anemioideae by *Mohria* or certain members of *Anemia* itself. The only presumed primitive or intermediate conditions found in Ophioglossaceae are occasional forms or terata in which the sporangia are borne upon partly or fully developed lamina. This is especially well shown in certain species (e.g., *Botrychium matricariifolium* A. Br. and *B. simplex* E. Hitchc.) in which a percentage of every population shows sporangia arising from the sterile segment margins.

Sporophylls which have the *encapsulated* or *angiosporangial condition* are especially well developed in Plagiogyriaceae and Aspleniaceae subf. Blechnoideae. In these ferns the sporangia are covered, at least partially, by the inrolling of the pinna margins. They are protected until they are fully mature and ready to discharge the spores. To study early stages of sporangial development it is necessary

to cut away or pull back the folded-over lamina. The most highly evolved encapsulated structures are those of the onocleoid ferns, especially *Matteuccia* and *Onoclea*, in which the sporophyll capsules do not open until months after the sporangia have matured.

Fertile-sterile differentiation at the histological level has been largely uninvestigated and we are currently trying to determine the scope of the anatomical changes associated with sporophylls. By using the frequent intermediates that occur as abnormalities in many dimorphic taxa, it is possible to detect gradients and establish homologies. Techniques of clearing and staining portions of the leaves are especially suited to this type of study. A brief summary of our observations is as follows: Narrowing of the segments of sporophylls is accomplished by the progressive reduction of the lamina until, in extreme cases like the botryoidal types described above, the axes become terete and there is no trace of laminar wings. Associated with this there is a large increase in the ratio of over-all surface to volume, allowing for more rapid drying. With reduction in lamina we usually notice an increase in the width of the vein intervals and a simplification of the vein pattern. The latter is accomplished by eliminating some of the vein branchings and most or all of the areoles, as in *Lorinseria areolata* (L.) Presl (Blechnoideae) and *Onoclea sensibilis* L. and *Onocleopsis hintonii* F. Ballard (Dryopteridoideae, Labouriau, 1958; Lloyd, 1971). In *Lomariopsis* the sporophylls have free-ending veins, lacking the marginal connections of the trophophylls (Holtum, 1939). Comparative investigations of the vein intervals of nearly two dozen taxa were made by Lommasson and Young (1971), but they did not compare conditions in sterile and fertile fronds.

There may be simplification in other laminar tissues as well. The epidermis may be softer in sporophylls than in trophophylls, and may tend to produce fewer stomates. The epidermal cells may be larger and straighter-walled. The mesophyll may have less elaborate spongy parenchyma that is composed of larger, thinner-walled cells. In most strongly dimorphic taxa, the cells lose their chlorophyll at maturity, appearing *en masse* a whitish, yellowish, or brownish color. Where the acrostichoid condition occurs, the sporangial initials are no longer localized in punctate or linear receptacles, but become spread over the abaxial surface, forming a continuous placental area both along and between the veins. As indicated earlier, the sporophyll venation of certain acrostichoid ferns may actually be more complex than that in the trophophylls.

The physiological study of sporophyll-trophophyll differentiation is still in its infancy. One thinks of such names as Labouriau, Sharma, Steeves, Sussex, Wardlaw, and Wetmore in connection with processes of initiation and development of fertile leaves. White (1971) has reviewed much of their work. There seems to be little question that formation of sporophylls is controlled hormonally, and that their timing is related to periods of light and perhaps heat, although there is a vast amount of research needed to clarify the factors involved. Various extraneous influences may interfere with the normal course of sporophyll development, causing intermediate fronds to form. There are scattered reports on effects of injuries brought on by such agents as fire, flood, mowing, destructive substances (e.g., tar), and the trauma of transplanting, in inducing intermediate fronds, but there are very few controlled experiments to warrant general conclusions. It does seem that destruction of many or all of the actively photosynthetic fronds of a given plant will have a tendency to produce imperfect expressions of sporophylls in the new crop of fronds. In *Polystichum acrostichoides*, the partially fertile, subdimorphic pinnae of "forma *incisum* (Gray) Gilbert" apparently result from abnormal new growth of late leaves after injury of the normal fronds of the season (Wagner, Farrar, and McAlpin, 1970).

In very strongly marked dimorphy, the fertile frond becomes less responsive to light and more responsive to gravity. The typical spreading orientation of the trophophyll in which the blade approaches a position perpendicular to the direction of light is absent in the sporophyll which is now so negatively geotropic that it becomes totally erect. A simple and quick experiment to demonstrate tropism of fertile parts may be made with *Botrychium virginianum* (L.) Sw. If whole leaves, including both the fertile and sterile segments, are cut off at ground level during the active growing season before the sporangia have fully matured or discharged, and laid in pans of water in various positions, we have found that at room temperature in only 10 to 20 hours all of the fertile spikes will twist and become upright, no matter what the position of their associated sterile segments, illustrating dramatically the "urge" to raise the sporangia to the highest position possible.

The tissues of the sporophylls, being simpler than those of trophophylls and having a more flimsy structure, are more readily dried out. Their vertical position in relation to sun and wind, in contrast to the trophophylls which are closer to the substrate and more protected, also promotes dessication. Presumably the sporophylls have "cheaper construction" partly because they are more ephemeral and, lacking photosynthesis, have no value to the plant after their function of spore production is finished. Support by the rest of the plant is withdrawn when the sporophyll's job is done, and the fertile frond accordingly turns brown, dries out, and falls away. This is shown especially well in single hemidimorphic leaves. The differentiated fertile tips of *Osmunda regalis* and *Polystichum acrostichoides* dry up and die long before the sterile parts of the same leaf. In *Botrychium*, *Ophioglossum*, and *Anemia*, the photosynthetic pinnae continue to function as if nothing had happened, even though major parts of the leaf, the fertile segments, have collapsed and turned to twisted debris.

The seasonal timing of sporophylls and trophophylls may differ profoundly in taxa occurring in the same geographical areas and habitats. Nozu (1968) studied periodicity in Japan of members of nine genera with respect to sterile-fertile frond maturation, and reported that in a given species they may differ by as much as six months. Usually the sterile fronds mature first during the course of the year, but in *Osmunda japonica* Thunb. the fertile fronds mature a month or so earlier than the sterile.

A most curious state of affairs is found in the periodicity of *Botrychium lunarioides* (Michx.) Sw., a rarity of the southeastern United States known as "Winter Grapefern." The frond arises above ground in November and the sterile segment expands to its full size by sometime in January. The fertile segment, on the contrary, remains curled over at the ground level and stays soft and meristematic for nearly three months, only expanding and become erect in March. Spore discharge occurs in late March and then the entire leaf, including both fertile and sterile segments, dies in April. The plants are dormant, and completely buried under ground, from April to November.

Of what adaptive value is fertile-sterile leaf dimorphism? It is found in plants of such widely different habits and habitats that it is practically ubiquitous. The condition is found in giant ferns (e.g., *Acrostichum*) and midget ferns (e.g., *Peltapteris*), in thick-textured ferns (e.g., *Polystichum*) and thin-textured ones (e.g., *Trichomanes*). Dimorphy occurs in ferns with simple leaves (*Pyrrosia*) and with compound leaves (*Maxonia*). It exists in taxa that are terrestrial, taxa that are epiphytic and taxa that are aquatic. It is found in taxa with upright stems, with creeping stems, and with climbing stems. Xerophytes and hydrophytes, arctic and tropical ferns — all have dimorphic representatives, the common species as well as the rare.

For what ecological reasons has dimorphic evolution occurred in such a gamut of ferns? One can, of course, ask the same question regarding other pteridophytes — *Equisetopsida* and *Lycopodiopsida* — which have made analogous changes of shoots rather than leaves. In all likelihood, similar forces have operated to produce strobili (analogous to apically hemidimorphous fronds) and whole fertile shoots (analogous to fertile-sterile segregation of whole fronds, for example *Equisetum arvense* L. and *Lycopodium carolinianum* L.).

Some major extrinsic factors to take into account are seasonality, radiant energy (e.g., heat, light), role of air and water, and biotic factors (e.g., shading, grazers, fungi). The plant functions of most importance here are photosynthesis, spore production, and spore dispersal and establishment.

All of the following adaptations may contribute to the differentiation of sterile and fertile fronds:

1. To elevate spores of the fertile fronds into the wind stream for maximum dispersal.
2. To permit more extreme drying effects to enable sporangia to open and close efficiently.
3. To spread out photosynthetic blades in horizontal positions for maximum reception of light.
4. To place photosynthetic blades in most humid surroundings to counteract water loss.
5. To bring photosynthetic blades closer to the substrate where there are higher carbon dioxide concentrations during day time.
6. To enable differentiation of seasonal timing for most favourable period for spore reproduction and most favourable period for vegetative assimilation.
7. To separate fertile from sterile parts if one or the other is more liable to grazing or fungal attack.

Most authors agree that sporophylls tend to bring the spores into a position where they can better be carried away by the wind. Holttum (1938) describes the common situation which "takes the form of a somewhat contracted lamina in the fertile fronds, which stand erect, on longer stipes than the broader sterile fronds which bend away in a rosette around them. ... This form of dimorphism undoubtedly helps the distribution of spores, raising the sporangia well above the surrounding leaves and exposing them to drier air and any slight wind that may exist."

Copeland (1906) emphasized the drying aspects in his analysis. In his words, "Dimorphism, whether merely begun, or highly developed, whether a character of whole fronds or of their parts, has in all cases the object of permitting the proper dryness of the mature sporangia without an improper desiccation of the vegetative structures. This is done by merely raising the reproductive structures farther above the substratum; or (rarely) by special structural devices, such as notched margins; by a restriction of the assimilating surface of the reproductive frond or region, so that it may be sacrificed in emergency; or by a more complete elimination of the vegetative structures in constitutionally ephemeral fertile fronds."

As already stressed, origin of sporophylls is accompanied often by increasing divergence or specialization of the trophophylls or trophophyllary blade parts. This specialization invokes progressive broadening of the blade together with re-orientation into spreading or horizontal position. The blade becomes shorter and if the fronds are clustered a rosette is formed (Fig. 2, D). In long-creeping rhizomes, the much reduced trophophylls are scattered and often cling to the substrate. The modification of the trophophylls provides maximum photosynthetic surface for the area of the blades and orients them so that they have a moister,

more protected environment. Under some circumstances, greater assimilation of carbon dioxide may be possible due to diffusion from the substrate of the respiratory products of bacteria, fungi, animals, and roots.

We need to know more about optimal times of appearance of sporophylls and trophophylls. Time of spore production, for example, may be highly adaptive, but we will not know this until we understand more about life cycles in the natural environment. In the Great Lakes area of North America, Hill and W. Wagner (1974) determined that thin-walled green spores are discharged in the spring and very thick-walled, non-green spores are discharged in the fall for the most part. This may have to do with germination and establishment, as the former group of spores are adapted for quick germination on mineral medium and the latter for slow germination on organic medium. The best season for release of thin-walled spores may be the spring when the greatest moisture and rainfall are available. Comparable conditions prevail in the tropics with respect to wet and dry seasons.

Drought conditions in tropical dry seasons may call forth extreme adaptations of the trophophylls, exaggerating those described above, as found in *Anemia* Sect. *Trochopteris* (*A. elegans* (Gardn.) Presl, *A. eximia* Taubert) with extremely small, flat laminae (cf. Mickel, 1962). The polypod, *Microgramma heterophylla* (L.) Wherry illustrates an elaborate form of heterophylly in a vining fern. This tropical American fern grows over dry limestone rocks and produces short, clasping, ovate leaves with blunt tips, in contrast to a more upright, elongate form of sterile leaf, and the long, erect, narrowly lanceolate fertile leaves. The completely flat, rosette-like sterile segment of the winter grapefern, *Botrychium lunarioides*, is probably adapted to growth only during winter months and is a device to capture maximum heat and light as well as to protect the tissues from sudden drying or cold shocks.

Whether or not sporophyll-trophophyll divergence has adaptive value with respect to parasites is presently purely speculative, but such a possibility should not be ignored. Collectors notice frequently, especially in the tropics, that soral structures seem to be especially liable to molds and to tiny insects that feed upon the spores and sporangia. Conceivably there are adaptive advantages to isolating the parts most likely to be eaten from those which photosynthesize. There is also a chance that the eating of sori and fertile pinnae by small animals may play some role in dispersal, especially of those spores that germinate beneath the soil or under leaf litter.

Although the onocleoid ferns are commonly cited by morphologists to illustrate foliar dimorphy, they are, in fact, unusual and not typical in several respects. Lloyd (1971) in his recent monograph of the systematics of the onocleoid ferns compared the fertile and sterile fronds of the three genera involved, but he did not compare them with other fern genera. Too little is known as yet about the rare Mexican genus *Onocleopsis* in its natural setting to evaluate it, but the two other genera, *Onoclea* and *Matteuccia*, show a number of unique features: The fertile leaves are (1) shorter than the sterile or equal to them, (2) their tissues are more dense and sclerified, (3) the sori, which are indusiate, are tightly encapsulated at maturity, and (4) the sporophylls persist much longer than the sterile fronds, which are early-deciduous in the autumn. What governs the final opening up of the bead-like pinnules is unknown, but in the eastern United States and Canada, where there is a strong winter-summer seasonality, the fertile units remain rigidly closed during the non-growing season and spore discharge is prevented. The hard, upright fertile leaves persist through the winter, covered with, or protruding through, the snow. The spores within stay green during their winter dormancy, and when they are released early in the spring they are ready to germinate immediately, thus taking advantage of the vernal moistness (Hill and W. Wagner, 1974). Although the sporophylls of *Onoclea* may sometimes equal or even surpass the

trophophylls in height, those of *Matteuccia* are relatively much shorter, one-third or less the length of the trophophylls. In August and September, the sporophylls of *Matteuccia* are hard to see, buried as they are among the tall trophophylls and the other foliage of their swamp habitats. But in mid-winter all or most of the herbaceous plants have wilted and collapsed, so that the sporophylls are entirely exposed and easily swept by the wind. However, the actual discharge does not occur until March and April. Obviously the morphological peculiarities of these plants are correlated with the unusual seasonality of their spore production and release.

DISCUSSION

The noted Cornell University morphologist of the first half of this century, Arthur J. Eames, entertained some unusual theories about foliar dimorphism. In general he read the sequence just the opposite of the traditional interpretation and the one adopted here. In Eames' words (1938), "The segregation of vegetative and reproductive functions in different parts of the leaf, or in separate leaves, represents undoubtedly a primitive condition ...; from this ancient dimorphism there has developed the condition — often called monomorphism — found in the majority of ferns, a blade serving for both vegetative and reproductive functions ... And from this there has developed a *new dimorphic condition* — fertile and sterile leaves separate; this change has taken place independently in various genera ... " He thus postulated "ancient" dimorphism, which is the primitive state, leading to monomorphism, and then, once again to "modern" dimorphism. (Cf. his figure 175).

Eames cited three families — Ophioglossaceae, Osmundaceae, and Schizaeaceae — as representing the primitive type. All of these are of the type referred to in this paper as having "botryoidal" sporangial arrangement. Those of "Polypodiaceae" (i.e., all higher leptosporangiate ferns) represent Eames' "modern" type. We are not clear, however, upon what evidence he based his conclusions. The Ophioglossaceae are so isolated and so lacking in fossil evidence that we can only reason about what its course of evolution has been. We assume that it was derived from monomorphic fern-like plants because of analogies with repeated evolutionary sequences that we know in other groups. With respect to Osmundaceae, Miller (1971) concludes that "isomorphism represents the primitive state, incomplete dimorphism (only certain pinnae of a fertile frond modified for sporangia formation) is intermediate, and complete dimorphism is advanced," and he calls attention to the fact that fragments of laminate fronds bearing osmundaceous sporangia occur mainly in Jurassic sediments but range throughout the Mesozoic. Miller notes that "such fronds are generally included in the form genus *Todites*." Even though dimorphic pinnae in Osmundaceae were also found as early as the Jurassic and Triassic, this does not mean that this condition was primitive, any more than in families known primarily only today in which both monomorphic and dimorphic pinnae occur.

Also, as regards Schizaeaceae, the investigations of Mickel (1962, 1967) tend to contradict the conclusions of Eames. Mickel states that "although the change to dimorphism seems spectacular, in *Anemia* it is apparently a relatively simple and taxonomically minor one, which has occurred at least twice in the genus." He explains the unique leaf structure of typical anemias with their upright fertile basal pinnae to be derived from the typical fern leaf with unmodified basal pinnae (as in the closely related genus *Mohria*), and he describes a series of species, beginning with *Anemia colimensis* Mickel, with nearly monomorphic pinnae, and continuing through more and more differentiated forms, that finally terminates in such end-points as *A. rutifolia* and *A. millefolia*.

In view of the patterns seen in Osmundaceae and Anemioideae, and the total pattern of ferns in general, it is unlikely that there are two kinds of dimorphism,

"primitive" and "modern," and that the latter arose from the former via a monomorphic stage. Such an hypothesis appears overly complex in the face of the over-all evidence. The hypothesis of one-way directionality is more economical and more probable. And when one considers the numerous analogous trends as are observed in other vascular plant orders such as Lycopodiales, Selaginellales, Equisetales and Cycadales, for example, the idea of reversal from dimorphic to monomorphic seems even less likely.

In his rather lengthy discussion of foliar dimorphy, Dickason (1946) wrote that "Evidently dimorphism has not arisen in response to any given set of environmental factors, and cannot be considered as adaptive." He based his conclusion, apparently, on the fact that dimorphy appears in plants of such widely different habits and habitats. Dickason was also concerned with the fact that "dimorphic and monomorphic species grow side by side." These conclusions are in keeping with a general negativism on Dickason's part with respect to adaptive values of most phylogenetic trends in ferns. He did concede, however, that dimorphy is an evolutionary advancement over monomorphy.

Whether Dickason's conclusion that there is no adaptive value in dimorphy is justified is questionable. Merely that foliar dimorphy occurs in a wide spectrum of habits and habitats does not necessarily militate against its being adaptive with respect to one or more of the factors outlined above. Furthermore, examples of non-adaptive and adaptive character-states in taxa that grow side-by-side are numerous in all plant communities. The point is that all plant species probably have mixtures of both adaptive and non-adaptive or neutral attributes.

Taxonomically there is no question that dimorphism is an extremely helpful character for making identifications. In *Genera filicum*, Copeland (1947) uses fertile-sterile dimorphism as a key character for over fifty genera. Nevertheless, it is not necessarily a valid character for establishing affinities or delimiting genera. For one thing, dimorphy is not a single character but an ensemble of different characters (Table 1), and any given expression invokes its own combination. Each manifestation must be analyzed accordingly. Furthermore, dimorphy has arisen in practically all families of ferns and in some of them probably several times. Table 2 summarizes the incidence in the various families and subfamilies of ferns. What is designated as "weak" involves only a few representatives of the taxon or only slight subdimorphism or both. "Strong" involves a majority of members and usually very distinctive sporophylls and trophophylls or well marked hemi-dimorphism. At the family level, dimorphy seems to be most pervasive in Ophioglossaceae, Plagiogyriaceae, Cheiropleuriaceae, Marsileaceae, and Salvinia-ceae.

In spite of the fact that dimorphy has been used to distinguish a number of fern genera, it is questionable whether it is of fundamental importance. Sometimes the dimorphic taxon is connected by intermediates to monomorphic taxa. Tagawa and Iwatsuki (Iwatsuki, 1961) erected the genus *Dimorphopteris* on the basis of its perfectly dimorphic fronds, the fertile pinnae so contracted as to be linearimoniliform. However, the type species, *D. moniliformis* from the island of Halmahera in the Moluccas has been shown by Holttum (1972) to be an extreme in a series of subdimorphic members of a section of the genus *Pronephrium*. Copeland, among others, paid considerable attention to sporophyll-trophophyll distinction in his classification, but this was apparently partially a result of his emphasis on convenience. In Table 3 are listed 12 genera (right-hand column) recognized by Copeland which may indeed be too little differentiated to justify separation from their parent genera.⁴

⁴ It may have some relevance that two recent students of the genus *Equisetum*, namely R. L. Hauke and C. N. Page, have rejected shoot dimorphism as a determining character for establishing sections and subgenera (Hauke, 1974).

The major taxonomic value of foliar dimorphy in ferns as a whole is at the species level. There are numerous examples of pairs of closely related species in which one member is essentially monomorphic and the other dimorphic. Such pairs deserve close examination; because of their genetic similarity their study may give us valuable insights into the evolutionary and adaptive significance of this phenomenon.

Table 1. Parallel and convergent changes associated with sporophyll-trophophyll differentiation. The primitive state for each character is undifferentiated or nearly so.

LEAF SIZE	Strongly unequal
ORIENTATION	Sporophyll erect, trophophyll spreading
PETIOLE LENGTH	Unequal
BLADE OUTLINE	Sporophyll narrow, trophophyll wide
BLADE CUTTING	Sporophyll usually more divided; trophophyll usually less divided (but exceptions)
LAMINAR WEBBING	Sporophyll with reduction or loss of lamina; trophophyll unchanged or with increase
LAMINAR MARGINS	Sporophyll commonly smoother; trophophyll more toothed
VENATION COMPLEXITY	Sporophyll most commonly simplified by vein loss; trophophyll more complex
VEIN INTERVAL	Sporophyll veins more remote; trophophyll veins more approximate
MESOPHYLL	Sporophyll non-green, soft; trophophyll green, more compact and rigid
EPIDERMIS	Sporophyll with fewer stomates and larger, smoother-walled cells; trophophyll with normal epidermis
SORIATION	Sori concentrated, often confluent into acrostichoid condition or grouped into botryoidal condition
ENCAPSULATION	Sporangia, at least while young, covered by rolled lamina
SEASONALITY	Sporophyll separated from trophophyll in time of appearance, usually earlier but may be later
DURATION	Sporophyll short-lived; trophophyll long-lived. Rarely otherwise

Table 2. Parallel and convergent evolution of foliar dimorphy in ferns. Relative incidence and main types in different families or subfamilies. Letters refer to dimorphic types in Figure 1.

ABSENT TO WEAK	MODERATE	STRONG TO COMPLETE
Marattiaceae (D)	Polypodioideae (B, D)	Ophioglossaceae (C) ¹
Gleicheniaceae	Lygodioideae (B)	Osmundaceae (B, D, E)
Matoniaceae	Dryopteridoideae (B, D, F)	Plagiogyriaceae (D)
Dipteridaceae	Blechnoideae (D)	Anemioideae (C) ²
Loxogrammeoideae		Ceratopteridoideae (D)
Grammitoideae (B, D)		Marsileaceae (C) ⁴
Schizaeoideae (D) ³		Salviniaceae (D) ⁵
Adiantoideae (D)		
Vittarioideae		
Cyatheoideae		
Hymenophylloideae		
Lindsaeoideae		
Asplenoideae		
Azollaceae		

¹ Fertile spike composed of fused basal fertile pinnae.
² Fertile basal pinnae not fused, except in some cases to the petiole.
³ Fertile blade drastically reduced and petiole exaggerated. Sterile petioles maintained at maturity in *Schizaea pusilla* Pursh.
⁴ Type "C" if sporocarps are modified fertile pinnae.
⁵ Sporophyll is the immersed root-like leaf.

Table 3. Genera of close affinity which were discriminated by Copeland (1947) on the basis of fertile-sterile leaf dimorphism.

MONOMORPHIC OR SUBDIMORPHIC PARENTAL GENUS	DIMORPHIC SEGREGATE
POLYPODIACEAE	
Pleopeltis	Lemmaphyllum
Pleopeltis	Marginariopsis
Colysis	Dendroglossa
Aglaomorpha	Merinthosorus
Crypsinus	Pycnoloma
ADIANTACEAE S. 1.	
Pteris	Neurocallis
CYATHEACEAE S. 1.	
Trichomanes	Feea
ASPLENIACEAE S. 1.	
Phanerophlebia	Cyclodium
Ctenitis	Psomiocarpa
Tectaria	Tectaridium
Tectaria	Hemigramma
Tectaria	Quercifilix

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